

Kleptoparasitic behaviors of two orb-weaving spiders in webs abandoned by *Metleucauge kompirensis* (Araneae: Tetragnathidae)

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Abstract — To study the kleptoparasitic behavior of web spiders invading webs abandoned by adult female *Metleucauge kompirensis* (Araneae: Tetragnathidae), I investigated the numbers of prey insects and intruding spiders on host webs. *Tetragnatha praedonia* (3.0–9.0 mm long) and *M. kompirensis* spiderlings (1.0–1.5 mm long) invaded the host-absent webs in early morning. The number of insects in abandoned webs decreased rapidly in the morning because of theft by intruders. The number of intruders increased gradually as time progressed, and in the afternoon most of them constructed small webs inside the abandoned webs. Larger intruders often drove smaller ones away, and acquired more insects than the latter. Prey theft in unoccupied host webs may be an effective strategy to obtain prey, because these webs are not defended.

Key words — abandoned host webs, interference among intruders, prey theft, timing of intrusion

Introduction

Vollrath (1984) used the term “kleptoparasitism” to describe all interactions in which resources are removed or stolen from an owner. He considered the resources to be objects that could be carried, such as food or cover (e.g. shells in hermit crabs). Members of the arachnid genus *Argyrodes* are well known to be kleptoparasitic, as they invade the webs of other species. Most species of *Argyrodes* do not make their own webs, and they steal prey insects or web silk from other webs (Kullmann 1959; Exline & Levi 1962; Vollrath 1984, 1987). Although several species do construct their own webs, they do not capture prey on them (Vollrath 1984). The exceptions are *A. antipodiana* (Whitehouse 1986) and *A. trigonum* (Cangialosi 1997).

Solitary web spiders rarely intrude into webs made by other spiders found at typical densities (Enders 1974; Eberhard 1978; Nyffeler & Benz 1980). In contrast, intrusion into neighboring conspecific webs is often observed in communal or colonial species (Lubin 1974; Buskirk 1975a, b; Lahmann & Eberhard 1979; Rypstra 1979; Binford & Rypstra 1992). Such intrusion also occurs in solitary species living at high densities above streams (Yoshida 1977a, b; Nyffeler & Benz 1980). Some spiders capture prey insects in their own webs, but

also steal prey from the webs of other spiders. It is therefore interesting to determine the ecological conditions under which web spiders intrude onto the webs of other spiders.

Several orb-weaving spiders, especially *Tetragnatha praedonia*, frequently attempt to invade the webs of *Leucauge magnifica* and *Metleucauge kompirensis*, but prey theft is infrequent because of defense by the web owner (Yoshida 1977a, b). In this paper, I report kleptoparasitic behaviors such as prey theft in unoccupied webs by two orb-weaving spiders, *T. praedonia* and *M. kompirensis* (Araneae: Tetragnathidae), observed in the abandoned webs of *M. kompirensis*, and discuss their kleptoparasitic strategies.

Materials and Methods

I conducted this investigation in the summers of 1980 and 1984 at the Hinokidani River, a 1- to 2-m-wide branch of the Kamo River in Kyoto, Japan. The surface of the stream was shaded in various places by vegetation growing on the banks, including trees (e.g. *Cryptomeria japonica*, *Chamaecyparis obtusa*, *Quercus serrata*), shrubs (e.g. *Lyonia neziki*), and herbs (e.g. *Boehmeria tricuspis*, *B. spicata*, *Erigeron linifolius*).

Adult female *M. kompirensis* construct horizontal orb webs (30–100 cm in diameter) above streams

(Yoshida 1977a). The webs are strong, and the viscid spirals are very adhesive (Yoshida 1999). This species hunts on the web mainly at night, and most spiders leave their webs to rest under leaves or twigs until the next morning. Most webs are destroyed before sunrise, but some are left intact during the day (Yoshida, unpublished data).

Tetragnatha praedonia usually capture prey on their webs, which are woven among twigs and herbaceous plants. Fewer webs are found in the daytime than at night. *T. praedonia* sometimes invades the orb webs of other species, such as *Leucauge magnifica* (Yoshida 1977a, b) and *Nephila clavata* (Yoshida 1986, 1988). They steal small insects from the host webs, or they build their own webs using the host webs as a kind of scaffolding (Yoshida 1986). Spiderlings of *M. kompirensis* usually build their webs among twigs and rocks above streams, both at night and during the day. However, they sometimes invade the webs of *Nephila clavata* and construct their webs among the barrier webs, or steal small insects from the orb webs of the hosts (Yoshida 1986, 1988).

On 5 August 1980, I selected ten abandoned webs of *M. kompirensis* and measured the major axis (R) and the minor axis (r) of each orb. Web area (S) was calculated using the formula $S = \pi Rr/4$. I then counted the numbers of prey insects and intruders on the webs, as well as the number of webs made by intruders within host webs between morning and evening.

On four days in August 1984, I removed *M. kompirensis* from their webs in the morning and observed the behaviors of intruders on the empty webs. Observed behaviors included prey-searching, prey theft, web construction, and interference among intruders. I estimated the body lengths of intruders by eye and distinguished each individual intruder by its size and relative position on the web.

Results

1) Diurnal changes in the number of prey insects and intruders in abandoned web

Prey observed in abandoned webs were primarily small dipterans (e.g. Chironomidae) 1.0–3.0 mm long, and ephemeropterans 3.0–5.0 mm long. The average number of insects per web was highest at the beginning of the observation period (08:10 am), although the standard deviation was large (mean \pm SD = 11.4 \pm 10.2). This number decreased rapidly to less than one half of the initial count by 09:40 (4.2 \pm 5.3). Then it decreased

gradually, and there were few insects per web in the afternoon (Fig. 1A). The average number of prey was 0.6 at 16:20. Thus, an average of 10.8 insects was lost from a web, probably because they had escaped or been eaten by intruders.

A total of 349 spiders invaded ten abandoned webs; 94% (325 spiders) were spiderlings of *M. kompirensis* and 6% (24 spiders) were juvenile *T. praedonia*. Fifty-five percent of *M. kompirensis* and 50% of *T. praedonia* constructed small orbs within the abandoned webs (Fig. 2). Intruders and their webs were few in number at 08:10, but then both increased (Fig. 1B). The maximum number of intruders in a web was positively correlated with the area of the abandoned web ($r^2 = 0.60$, $p < 0.05$, $n = 10$). The proportion of intruders with their own webs was <10% before 09:40, and then increased rapidly. More than 70% of intruders had webs after 15:00 (Fig. 1B).

Host spiders emerged from their resting sites at sun-

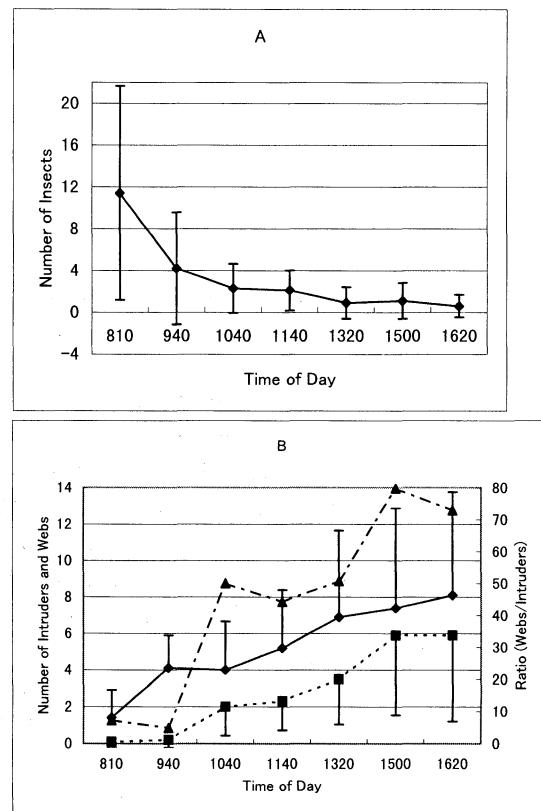


Fig. 1. A) Diurnal changes in the mean number of prey insects remaining in abandoned webs. B) Diurnal changes in the mean number of intruders (diamonds) and intruder webs (squares). Bars indicate standard deviations. Triangles represent the percentage of intruders that had own webs.

set, returned to their webs, destroyed them, and then made new webs. During this process, all of the intruders were driven away.

2) Behaviors of intruders following host removal

In August 1984, I observed the behaviors of intruders in empty webs (one web per day) from which the host spiders were removed. There were no intruders in the host webs when the hosts were removed. The two species invading the empty webs were *M. kompirensis* spiderlings (1.0–1.5 mm long), and juvenile *T. praedonia* (3.0–9.0 mm long). Various types of behavior were observed, including prey-searching, web ingestion, web construction, and interference among intruders. Intruders located prey insects remaining in empty webs, mainly while walking within the webs; however, they sometimes found insects while destroying small parts of the webs, in which case they consumed the insects and the silk. On 6 and 9 August, of 56 insects stolen by *T. praedonia*, 79% were found while walking and 20% while ingesting silk.

On 11 and 12 August, I observed the webs from morning until evening and recorded 57 spiders invading the webs; 79% were *M. kompirensis* and 21% were *T. praedonia*. Of the prey insects left in the host webs, 25% were eaten by *M. kompirensis* and 64% by *T. praedonia*. Eleven percent were lost for unknown reasons, probably because I had not observed the prey thefts. None of three

T. praedonia webs built within the host webs captured prey, while four of the 24 *M. kompirensis* webs captured an insect (Table 1).

The number of prey thefts was significantly correlated with the body length of *T. praedonia* (Spearman's rank correlation coefficient, $r_s = 0.73$, $p = 0.007$, $n = 12$). The three largest individuals of *T. praedonia* stole 24 insects (60% of total insects captured by the host webs) on 11 August. Similarly, the two largest *T. praedonia* stole 18 insects (45% of the total) on 12 August (Fig. 3). Prey insects left in host webs were sto-

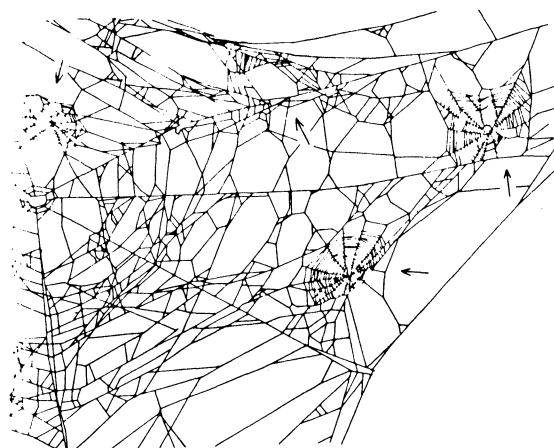


Fig. 2. Intruder webs made within an abandoned web. Four tiny webs are shown by arrows (drawn from a photo).

Table 1. Numbers of intruders and prey thefts, and numbers of intruders' webs and prey insects captured by intruder's webs. Numerals in parentheses show the percentages. T: *Tetragnatha praedonia*, M: *Metleucauge kompirensis*.

Date	No. of Intruders		No. of Prey Thefts			Number of Webs		Prey captured	
	T	M	T	M	unknown	T	M	T	M
11 Aug.	9(39)	14(61)	33(82)	3(8)	4(10)	2	5	0	0
12 Aug.	3(9)	31(91)	18(48)	17(42)	5(13)	1	19	0	4
Total	12(21)	45(79)	51(64)	20(25)	9(11)	3	24	0	4

Table 2. Diurnal changes in the number of prey thefts and that of prey captures by intruder's webs.

	11 Aug.			12 Aug.		
	7:30–10:30	10:30–13:00	13:00–15:30	8:00–11:00	11:00–13:30	13:30–16:00
<i>Prey Theft</i>						
<i>T. praedonia</i>	33	0	0	18	0	0
<i>M. kompirensis</i>	3	0	0	12	3	2
unknown	4	0	0	5	0	0
Total	40	0	0	35	3	2
<i>Prey Capture</i>						
<i>T. praedonia</i>	0	0	0	0	0	0
<i>M. kompirensis</i>	0	0	0	0	1	3
Total	0	0	0	0	1	3

len mainly during the three hours following host removal (Table 2). On 12 August, however, intruders stole four insects newly captured by the host web during the day.

Table 3 shows the frequency of interference patterns among intruders on the two days. The following patterns were observed: (A) the dominant intruder pursued or approached the subordinate, and the latter escaped; (B) the dominant intruder destroyed the web of the subordinate, and the latter escaped; (C) the dominant intruder pursued

or approached the subordinate, and the latter dropped from the web.

Intraspecific interference between two individuals of *T. praedonia* occurred 8 times, and interspecific interference between *T. praedonia* and *M. kompirensis* occurred 21 times. I did not count the frequency of intraspecific interference among individuals of *M. kompirensis*, because the interference was difficult to observe. Spiderlings of *M. kompirensis* were much smaller than juvenile *T. praedonia* and moved very slowly, so intraspecific interference may have been overlooked in most cases, especially when *T. praedonia* moved on an empty web.

Pattern (A) was observed both between two individuals of *T. praedonia* and between *T. praedonia* and *M. kompirensis*. On the other hand, patterns (B) and (C) were observed only between *T. praedonia* and *M. kompirensis*. The ratio of body lengths of *T. praedonia* to *M. kompirensis* was larger in pattern (C) than in the pattern (A); (*t*-test, $f=15$, $p=0.006$) (Table 3).

Discussion

1) Kleptoparasitic behavior in *Tetragnatha praedonia* and *Metleucauge kompirensis*

To what extent are *T. praedonia* and spiderlings of *M. kompirensis* kleptoparasitic? *T. praedonia* seems to have some kleptoparasitic habits, based on the following observations: 1) *T. praedonia* invades the webs of various species: *T. praedonia*, *M. kompirensis*, and *Leucauge magnifica* (Yoshida 1977a, b), *Araneus ventricosus* (Yoshida 1977b), *Nephila clavata* (Yoshida 1986, 1988), *Araneus cornutus* (Yoshida, personal observation), and the unoccupied webs of *M. kompirensis* (this study). 2) *T. praedonia* steal prey insects from host webs (Yoshida, 1977a, b, 1986, this study). 3) *T. praedonia* finds many insects while walking around on unoccupied webs, as shown in this study. This behavior seems to be effective in finding motionless small insects in large host webs. I never observed such prey-searching behavior when prey insects were captured in their own webs

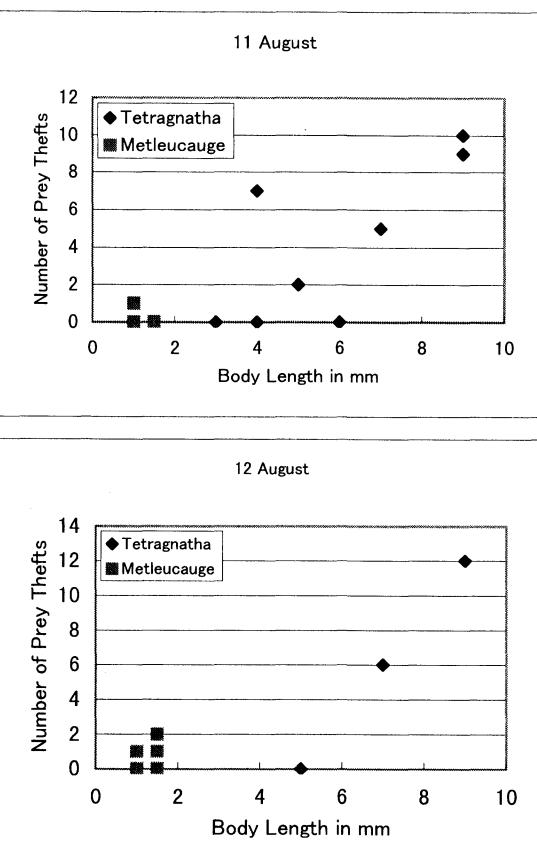


Fig. 3. The relationship between the body length of intruders and the number of insects they preyed on. Diamonds and squares represent *Tetragnatha praedonia* and *Metleucauge kompirensis*, respectively.

Table 3. Frequency of interferences among intruders. T: *T. praedonia*, M: *M. kompirensis*. Ratio BL shows the average \pm standard deviation of the ratio of the body length between two intruders.

Pattern of Interference	Behavior of Intruders		Combination		Combination		
	Dominant	Subordinate	T-T	Ratio BL	T-T	Ratio BL	Total
A	Pursuit or Approach	Escape	8	1.4 \pm 0.4	7	5.0 \pm 1.5	15
B	Web Destruction	Escape	0	—	3	7.0 \pm 1.7	3
C	Pursuit or Approach	Drop	0	—	11	7.4 \pm 2.0	11
Total			8		21		29

(Yoshida 1987). 4) *M. kompirensis* often overlooks the intrusion of *T. praedonia*, probably because they move more slowly on the host web than other intruding species (*M. kompirensis* and *L. magnifica*) of similar size (Yoshida, personal observation). Similarly, *M. kompirensis* spiderlings seem to have some kleptoparasitic habits, because they invade *N. clavata* webs (Yoshida 1986, 1988) as well as webs of conspecific adults (this study).

However, *T. praedonia* and *M. kompirensis* spiderlings are apparently different from most *Argyrodes* species, because they construct webs to capture prey insects. Most individuals capture prey insects with their own webs, so intrusion into other webs may be primarily because the densities of conspecific and/or heterospecific webs are high. Intrusion may be elicited when there are less scaffolds for web-making, or when there are many other webs near the web. Intrusion into neighboring conspecific webs is often observed in communal or colonial species (Lubin 1974; Buskirk 1975a, b; Lahmann & Eberhard 1979; Rypstra 1979; Binford & Rypstra 1992). Such intrusion also occurs in solitary species at high densities above streams (Yoshida 1977a, b; Nyffeler & Benz 1980).

2) Strategies of web spiders to capture prey insects

Web spiders can use three strategies to capture prey insects: 1) they capture prey in their own webs constructed among natural supports, such as twigs, herbaceous vegetation, or rocks; 2) they capture prey in their own webs built within host webs; and 3) they steal prey from host webs. Which strategy is best seems to depend on conditions, such as the availability of web sites for constructing their own webs, the cost of web construction, the density of host webs, the number of insects left in a host web, and the defense of the host.

Prey theft may be a better strategy for web spiders than prey capture in their own webs, because the cost of web construction is eliminated; however, spiders usually defend their webs (Lubin 1974; Buskirk 1975a, b; Rypstra 1979; Vollrath 1984). Adult female *M. kompirensis* also defend their webs. They usually make their webs in the evening, at which time *T. praedonia* frequently try to invade the webs. Intrusions are usually unsuccessful, because *M. kompirensis* defend themselves, although *T. praedonia* sometimes steal small insects at the periphery of the webs (Yoshida 1977a, b). *T. praedonia* also invades the webs of *Nephila clavata* located above a stream. They usually remain within the barrier webs, but sometimes invade the orb webs of the hosts. In the study of prey capture of spiders (Yoshida

1986), *T. praedonia* stole only one small insect during 2.3 days of observation (0.4 insects/day). This low value was probably because the orb web was defended by *N. clavata*. In contrast, *T. praedonia* steals more insects from the unoccupied webs of *M. kompirensis*, as shown in this study. Thus, prey theft from unoccupied webs seems to be more advantageous than that from occupied webs, since the former are not defended.

In this study, two types of competition were observed. One was direct interference competition, which occurred frequently. Intraspecific interference has also been observed in *Argyrodes antipodiana* within the host web (Whitehouse 1997; Whitehouse et al. 1994). The other form of competition was exploitation. For example, on 11 August 1984, all prey insects had been stolen by 10:30, so spiders intruding after 10:30 could not acquire any insect. The earlier a spider intruded, the more likely it was to obtain more prey insects. This was more important for smaller spiders, because they were often driven away by larger ones.

Although *T. praedonia* and *M. kompirensis* competed with conspecifics, they also competed with each other. Larger numbers of *M. kompirensis* invaded host webs and stole more prey insects where there were fewer *T. praedonia*.

If web spiders capture prey insects with their own webs, they must acquire enough energy by prey capture to offset the cost of web construction. Consequently, it is advantageous for spiders to build their webs where prey insects are abundant. Adult female *Leucauge magnifica* built webs above a stream and on its banks, and captured more insects above the stream (mean \pm S D = 34.4 \pm 54.8 insects/web/day) than at the banks (4.0 \pm 3.3 insects/web/day) (Yoshida 1977a). Prey were certainly more abundant above the stream than above the banks. On the other hand, adult female *M. kompirensis* spun webs exclusively above the stream, and the web density was positively correlated with the prey capture rate (Yoshida 1977a). Thus, *M. kompirensis* seems to select more productive web sites.

Web-making within the unoccupied webs of *M. kompirensis* seemed to be disadvantageous, because few insects were captured in the webs of intruders during the daytime, and because the host destroyed all the intruder webs in the evening. Many intruders made their webs inside a host web. Web-making occurred when few insects were trapped in the host web. Web-making behavior inside the host web seemed to be elicited when intruders were unable to find any insect there. *M. kompirensis* spiderlings also invaded *N. clavata* webs made above a

stream. The spiderlings constructed their webs among the barrier webs of the hosts, or they invaded the orb webs and stole prey insects. Intruder webs were not destroyed by *N. clavata*, because the host usually stayed inside the orb web. *M. kompirensis* obtained more insects with their own webs (2.5 insects/day) than through theft in orb webs of *N. clavata* (0.9 insects/day) (Yoshida 1986). Thus, the former strategy may be advantageous in this case. More insects may be captured by the webs of *N. clavata* made above streams than at banks.

Web spiders can capture prey insects with their own webs spun across natural supports, but none of the 34 *M. kompirensis* spiderling webs constructed among natural scaffolds contained prey insects in August 1984. These tiny webs were found among rocks and twigs above a stream, mainly near the banks. Few webs were found in the central open spaces above the stream, probably because these gaps were too broad to spin the web (Yoshida, personal observation). Therefore, the spaces near banks may be less productive than central open spaces.

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Acta Arachnologica Vol. 50, No. 1 掲載論文の和文要旨

トリノフンダマシはガを誘引しない (pp. 1-4)

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トリノフンダマシ類は、おもにガを捕食することが知られている。これらのクモがナゲナワグモのように特定の雄のガを誘引しているかを確かめるため、クモに捕獲されたガと飛翔中のガを採集し種組成と性比を調べた。餌となったガはさまざまな種の雌雄から構成されており、性比は 0.77 で雌に偏っていた。また、餌となったガと飛翔中のガの性比に違いはみられなかった。したがって、トリノフンダマシ類は特定の雄のガを誘引していないと考えられる。

タニマノドヨウグモの放置網における円網を張るクモ 2 種の盗み寄生的行動 (pp. 5-11)

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タニマノドヨウグモの放置網における円網を張るクモの盗み寄生的行動を調査するため寄主の網にかかる昆虫の数を調べた。アシナガグモ (体長 3-9 mm) とタニマノドヨウグモの幼体 (1-1.5 mm) が早朝に寄主が不在の網に侵入した。侵入者の盗みによって放置網上の昆虫の数は午前中に急速に減少した。侵入者の個体数は徐々に増加し、午後にはそれらのほとんどは放置網の中に小さい網を構築した。大型の侵入者は小型の侵入者を追い出し、より多くの昆虫を獲得した。寄主による防衛がないので、放置網における餌盗みは餌獲得には効果的な戦略かもしれない。

南西諸島産コガネヒメグモ属およびツリガネヒメグモ属 (クモ目: ヒメグモ科) の 2 新種 (pp. 13-16)

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南西諸島産のヒメグモ科の 2 新種を、*Chrysso sasakii* オキナワホシミドリヒメグモ (新称、沖縄島、屋久島産) および *Achaeareana projectivulva* トガリヒメグモ (新称、沖縄島産) の名前で記載した。

韓国より得られた *Dyobelba* 属の 1 新種 (ダニ亞綱: ササラダニ目: ジュズダニ科) (pp. 17-22)

バヤルトグトホ バダムドルジ¹, 崔 星植², 青木淳一³ (¹モンゴル国立大学生物学部動物学研究室; ²圓光大学校農科大学; ³神奈川県立生命の星・地球博物館)

韓国より得られた *Dyobelba* 属の 1 新種を記載した。*Dyobelba paucituberculata* sp. nov. は、次の点によって同属の他種から区別される: 前体部背面隆起 (prodorsal enantiophyses) B, D, 腹面内隆起 (epimeral and dorsosejugal enantiophyses) E2, V, および脇突起 (discidium) を完全に欠くこと, 基節板毛の数本 (第 1-第 3 列 D, および 4b) の基部に微小突起を持つこと, 第 IV 脚転節に 2 本の毛を持つこと。*Dyobelba* 属の識別点およびこれまでに知られている本属の分布について記述した。

台湾初記録のカワリアシダカグモ属 (新称), コアシダカグモ属, ミナミアシダカグモ属および 4 新種の記載 (クモ綱: クモ目) (pp. 23-31)

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台湾からアシダカグモ科の 4 新種を以下のように命名して記載した: *Pseudopoda serrata*, *Pseudopoda recta*, *Sinopoda exspectata*, *Olios sculptor*. これら 3 属とも台湾から初記録となる。またアシダカグモ *Heteropoda venatoria* (Linné 1767) の 1 採集記録も報告した。

日本産のモリヒメグモ属, ハガタグモ属, カガリグモ属およびオオノヒメグモ属 (クモ目: ヒメグモ科) (pp. 33-51)

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日本産のヒメグモ科モリヒメグモ属, ハガタグモ属, カガリグモ属およびオオノヒメグモ属に検討を加え、これら 4 属に含まれる 17 種に検索表および簡単な記載をえた。北海道大雪山高山雪田群落で採集されたモリヒメグモ属の 1 新種 *Robertus yasudai* new species (ヤスダモリヒメグモ, 新称) を記載し、中国産の *Enoplognatha lordosa* Zhu & Song 1992 (コガタコノハグモ, 新称) を日本から新たに記録した。*Enoplognatha abrupta* (Karsch 1879) new combination (カレハヒメ